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Posterior Cingulate Cortex Integrates the Senses of Self-Location and Body Ownership

Highlights

- We used an out-of-body illusion to perceptually teleport participants during fMRI
- Self-location could be decoded from parieto-cingulate-hippocampal activity
- Ownership of a seen full body was associated with premotor-intraparietal activity
- The posterior cingulate plays a key role in merging self-location and body ownership

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In Brief

Guterstam et al. used an out-of-body illusion to perceptually teleport subjects during fMRI. Self-location could be decoded from parieto-cingulate-hippocampal activity; posterior cingulate activity reflected integration of self-location and body ownership, suggesting a key role in the coherent experience of the bodily self in space

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Posterior Cingulate Cortex Integrates the Senses of Self-Location and Body Ownership

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SUMMARY

The senses of owning a body and being localized somewhere in space are two key components of human self-consciousness. Despite a wealth of neurophysiological and neuroimaging research on the representations of the spatial environment in the parietal and medial temporal cortices, the relationship between body ownership and self-location remains unexplored. To investigate this relationship, we used a multisensory out-of-body illusion to manipulate healthy participants' perceived self-location, head direction, and sense of body ownership during high-resolution fMRI. Activity patterns in the hippocampus and the posterior cingulate, retrosplenial, and intraparietal cortices reflected the sense of self-location, whereas the sense of body ownership was associated with premotor-intraparietal activity. The functional interplay between these two sets of areas was mediated by the posterior cingulate cortex. These results extend our understanding of the role of the posterior parietal and medial temporal cortices in spatial cognition by demonstrating that these areas not only are important for ecological behaviors, such as navigation and perspective taking, but also support the perceptual representation of the bodily self in space. Our results further suggest that the posterior cingulate cortex has a key role in integrating the neural representations of self-location and body ownership.

INTRODUCTION

We experience our body as a physical entity with a specific location in the external space. For instance, when sitting at your desk, you are aware of your body and its approximate position with respect to objects and the spatial boundaries of the room [1]. This sense is essential for our interactions with the outside world [2] and has long been regarded among philosophers and psychologists as a fundamental aspect of self-consciousness [3, 4]. Recently, neuroscientists have started to explore its neural correlates and have highlighted two factors, implemented in partially distinct neural substrates, as key to bodily self-consciousness: the feeling that the body is part of the self (body ownership) and the experience that the body is located somewhere in space (self-location) [5–7]. This view is supported by the existence of neurological impairments that specifically affect the sense of body ownership or the sense of self-location. For instance, patients suffering from asomatognosia fail to recognize their own limbs as part of the self [8], whereas focal epilepsy and electrical stimulation of the temporal and parietal cortices can sometimes induce out-of-body experiences (OBEs), in which the perceived self-location is temporarily detached from the patient's physical body [9–11]. Although the existence of these conditions suggests that body ownership and self-location require intact neural processing in fronto-parietal and temporo-parietal areas, respectively, their underlying mechanisms and their relationship remain poorly understood.

Recent studies using perceptual illusions in healthy participants have demonstrated that multisensory integration of signals from the body viewed from the first-person visual perspective (1PP) is a key mechanism for the emergence of body ownership [12, 13]. The illusory experience that an artificial hand [14] or an entire body [13] is one's own is associated with increased activity in the premotor-intraparietal regions [13, 15]. These areas integrate visual, tactile, and proprioceptive information and contain neurons with visuo-tactile receptive fields anchored to a portion of the body surface and its surrounding (peripersonal) space [16, 17]. Neuronal populations in these areas construct multisensory representations of the boundaries of one's body and are ideally suited to support the feeling of body ownership [7, 18, 19]. Conversely, theories regarding the neural mechanisms underlying the sense of self-location draw primarily from the study of spatial navigation in rodents and virtual navigation in humans. Abundant evidence from such studies indicates that the medial temporal and posterior parietal cortices are involved in the construction of internal representations of an individual's spatial location [20–22] and head direction [23–27]. However, it remains unclear how these representations relate to the perceptual experience of self-location and the representation of one's own body.

In light of the above, we set out to investigate the neural representations of self-location and body ownership and their functional interplay. We manipulated these factors by making use of a perceptual out-of-body illusion [12]. In the original experiment, the participants sit on a chair and wear a set of head-mounted displays (HMDs) through which they observe the real-time 3D video feed from a pair of cameras located 2 m behind them. The experimenter then synchronously touches the participant's chest, which is hidden from view, and the space just below the cameras with two identical small objects. This mode of visuo-tactile stimulation leads to the illusory experience of

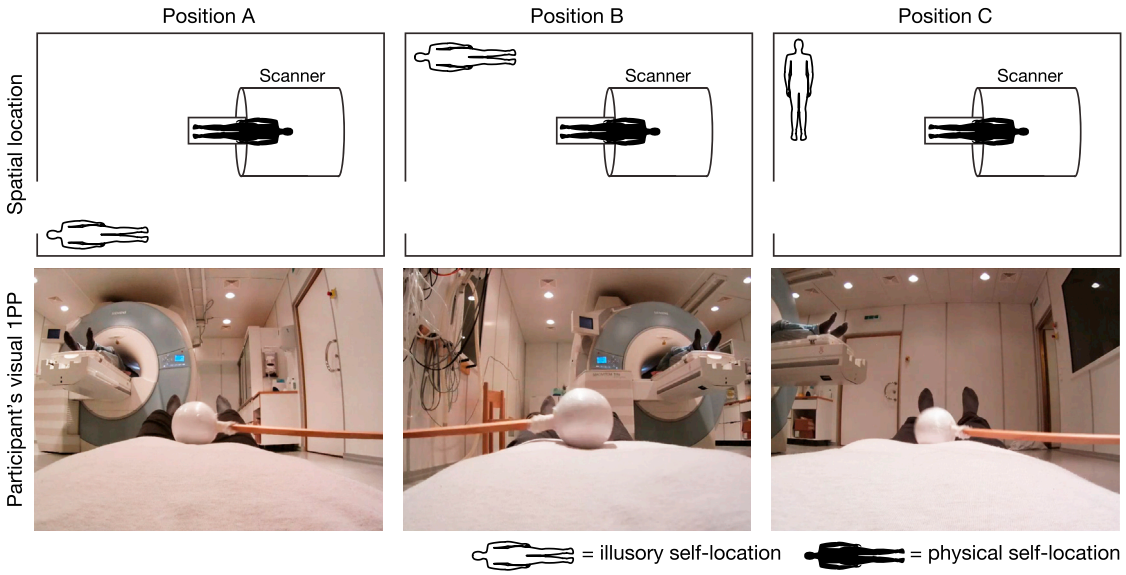

Figure 1. Experimental Setup

The participants were positioned inside an MRI scanner and looked into a set of HMDs. The upper panels show a schematic map of the scanner room indicating the participants' physical self-location (black), as well as the illusory self-location (white) for positions A, B, and C. The lower panels show one sample frame from the stereoscopic visual stimuli presented to the participants in the HMDs (only the left eye's image is shown here) for each position. In the HMDs, the participants viewed their real body (from the third-person perspective [3PP]) lying in the scanner and the stranger's body (from the 1PP) being touched by a white spherical object, while receiving synchronous (illusion condition) or asynchronous (control) tactile stimulation. 1PP, first-person perspective. See also Figure S1 and Movie S1.

being physically located at the position of the cameras and that the observed real body is no longer part of the self [12, 28]. Crucially, the delivery of asynchronous touches significantly reduces the illusion and allows for the comparison of otherwise equivalent conditions [12, 28]. Here, we adapted the out-of-body illusion to a supine, head-tilted posture inside a MRI scanner. This experimental setup allowed us to manipulate the sense of body ownership and study self-location by perceptually "teleporting" the participants between locations within the real-world scanner environment while recording brain activity using high-resolution fMRI (see the Experimental Procedures).

Fifteen healthy participants were positioned inside an MRI scanner with their head tilted forward while wearing HMDs. Through the displays, they viewed the scanner room and themselves in stereoscopic vision from the perspective of a stranger lying on the floor in one of three positions: positions A, B, and C (Figures 1 and S1). Positions A and B corresponded to two different corners of the room with identical head directions, whereas positions B and C represented perpendicular head directions in the same corner. To elicit the illusion of owning the stranger's body seen from the 1PP and being physically located in position A, B, or C, the experimenter applied synchronous touches to the participant's body and the corresponding location on the stranger's body (Figure 1 and Movie S1) [12, 13]. The touches delivered to the real body were hidden from the participants' view in the HMDs (see the Supplemental Experimental Procedures for details). For each position, we also included a control condition in which the touches occurred asynchronously to reduce the illusion.

This experimental design allowed us to test for changes in brain activity that reflect alterations in the feelings of body ownership, self-location, and the functional interplay between ownership and self-location. We conducted three main analyses. First, we estimated the main effect of visuo-tactile synchrony across positions to examine the activity related to the feeling of ownership of the stranger's body viewed from the 1PP [13, 15]. Second, to identify the neural substrates of the perceived self-location, we used multivoxel pattern analysis [29] to decode position A versus B (for perceived head direction, we decoded position B versus C) in the synchronous condition, using the asynchronous condition as a control for illusion non-specific effects. Finally, we investigated the neural interplay between the representations of body ownership and self-location by examining the illusion-induced changes in effective connectivity between the corresponding sets of brain regions.

RESULTS

Illusion Quantification—Behavioral and Psychophysiological Results

Before examining the fMRI results related to the illusion experience, we tested the efficacy of the experimental manipulation of body ownership and self-location [12, 28]. To this end, we conducted three behavioral experiments in parallel with, or immediately after, the brain-scanning sessions and quantified subjective and objective changes in the perceived self-location and body ownership. In a post-scan self-location task (see the Experimental Procedures and Figure S2A), we presented the participants with a map of the scanner room and asked them to rate how strongly they perceived themselves to be located in different candidate positions [28]. The results showed that the synchronous, as opposed to the asynchronous, condition

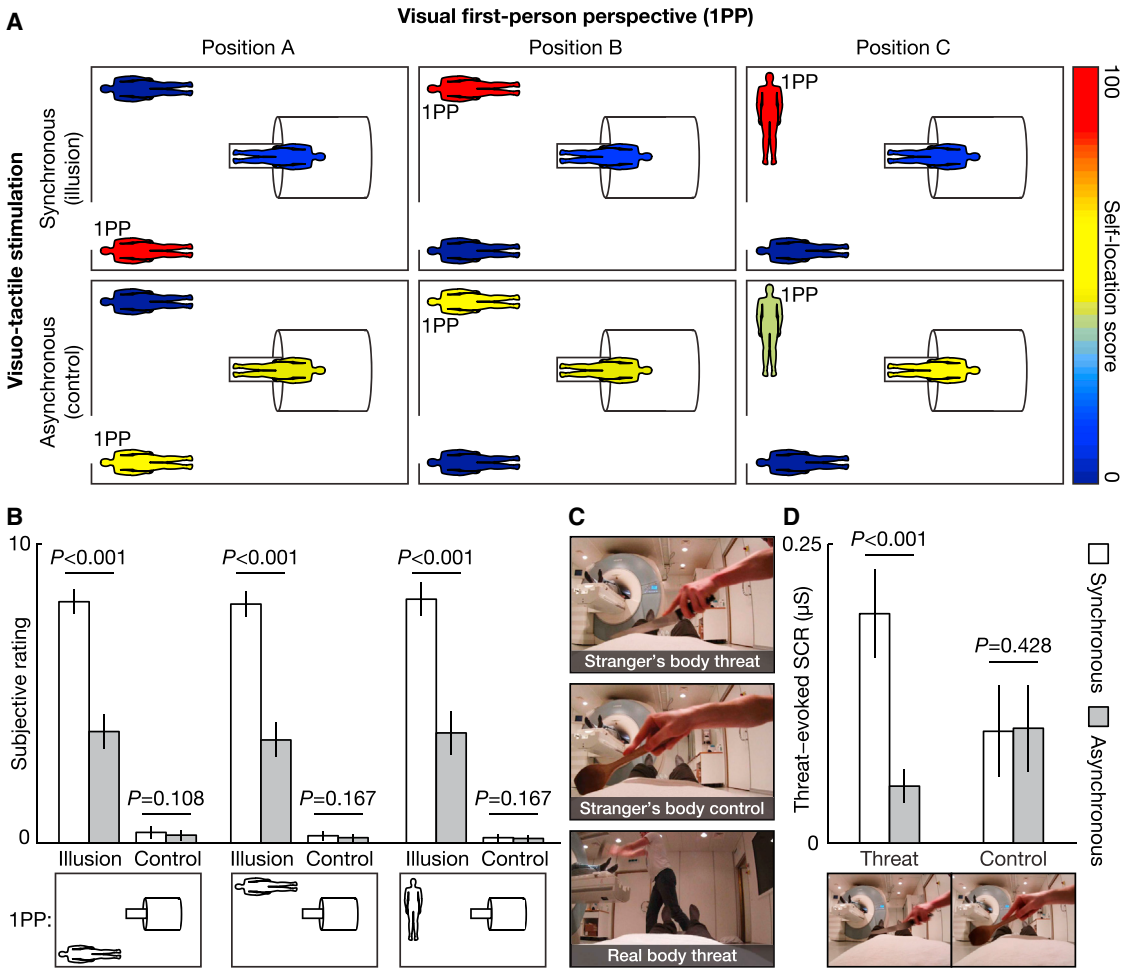

Figure 2. Behavioral Results

(A) The results of the post-scan self-location task revealed that the synchronous condition was associated with a strong sense of self-location in the out-of-body positions and a weak sense of self-location inside the scanner.

(B) Participants consistently rated statements reflecting the illusion experience, but not the control statements, as significantly higher for the synchronous, but not for the asynchronous, condition. See also Figure S2B for the ratings of each individual statement.

(C) Sample frames depicting the three different threat events.

(D) The SCR evoked by a knife, but not a spoon, threatening the stranger's body was significantly higher in the synchronous compared to the asynchronous condition.

Error bars indicate the SEM. See also Movie S1.

was associated with a strong and unambiguous sense of self-location in the out-of-body position and a weak sense of self-location in the veridical position inside the scanner ($p = 0.010$; Figure 2A). A separate post-scan questionnaire experiment confirmed that the participants vividly experienced ownership of the stranger's body in the out-of-body position (A, B, or C) during the synchronous, but not during the asynchronous, condition ($p < 0.001$; Figure 2B; see Figure S2B for the questionnaire statements).

Concurrently with the brain scanning, we examined the skin conductance response (SCR) evoked by physical threats directed toward the stranger's body and the real body (Figure 2C and Movie S1). Previous studies have shown that such SCRs can be used as an objective physiological proxy of body ownership [12, 28, 30]. In line with the subjective reports, we found that threatening the stranger's body with a knife elicited a significantly greater SCR in the synchronous compared to the asynchronous condition. Importantly, this was not the case when the knife was substituted with a neutral object such as a spoon ($p = 0.002$, interaction effect; Figure 2D). Moreover, we examined the blood-oxygen-level-dependent (BOLD) responses evoked by these threats in brain regions involved in the experience of fear and pain anticipation, as well as the SCR and BOLD responses to threats directed toward the real body, providing further psycho- and neurophysiological support for successful induction of the illusion (Figure S3).

Taken together, these behavioral, psychophysiological, and threat-evoked BOLD results are consistent with the notion that the illusion experience is dependent on temporally congruent visuo-tactile stimulation and involves ownership of the stranger's

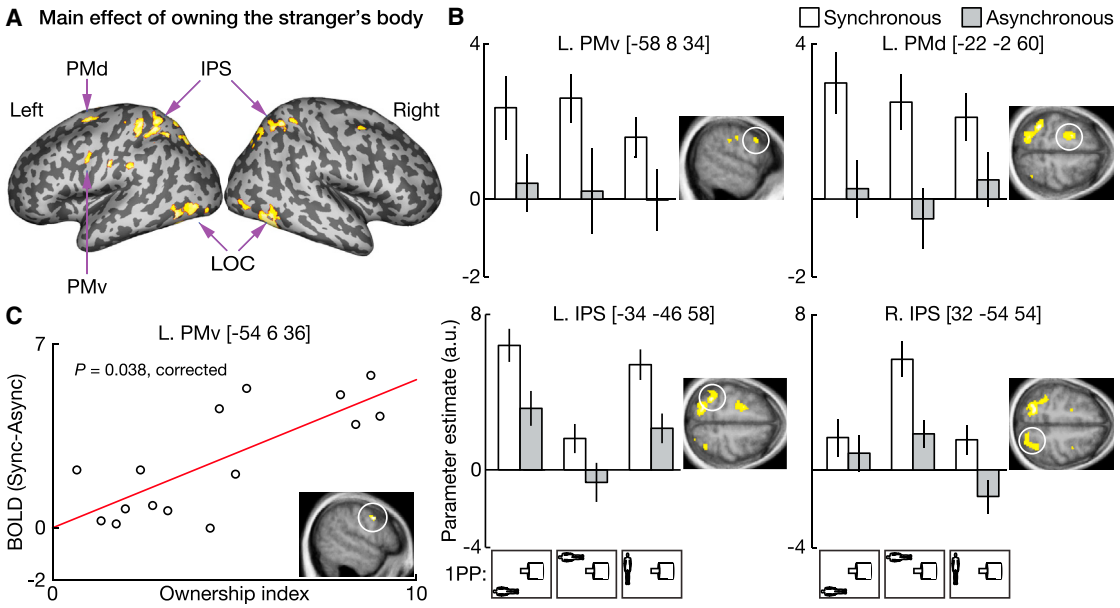

Figure 3. Body Ownership-Related Brain Responses

(A) The main effect owning the stranger's body viewed from the 1PP (synchronous versus asynchronous across positions) revealed significant activations in the premotor and posterior parietal areas related to multisensory integration of visual, tactile, and proprioceptive signals from the body. PMd, dorsal premotor cortex; PMv, ventral premotor cortex; IPS, intraparietal sulcus; LOC, lateral occipital cortex.

(B) The key activations in the PMd and PMv and the cortex lining the IPS were driven by a consistent synchronous versus asynchronous difference across the positions (see also Figure S3 for the threat-evoked fMRI activations). Error bars indicate the SEM.

(C) The level of activity in the left PMv reflected the subjectively rated strength of the feeling of ownership of the body seen from the 1PP across the three different positions.

For display purposes, the statistical threshold for the activation maps was set to $p < 0.005$, uncorrected. In (B) and (C), a white circle indicates a cluster containing a significant peak ($p < 0.05$, corrected).

body seen from the 1PP and a clear sense of self-location in the out-of-body positions. These findings support the feasibility of our approach of using this perceptual illusion to manipulate the senses of body ownership and self-location during fMRI.

Body Ownership-Related Brain Responses

Next, we characterized the BOLD responses associated with the feeling of ownership of the stranger's body viewed from the 1PP by computing the main effect of visuo-tactile synchrony across positions (see the Supplemental Experimental Procedures). This analysis revealed activations in key multisensory areas in the left premotor (ventral, $t = 3.11$, $p = 0.037$; dorsal, $t = 4.17$, $p = 0.002$, corrected) and bilateral intraparietal cortices (left, $t = 4.40$, $p = 0.001$; right, $t = 3.37$, $p = 0.019$, corrected) that have previously been associated with the feeling of ownership of an entire artificial body viewed from the 1PP [13] (Figures 3A and 3B). In addition, we reproduced a significant positive relationship between the level of activity in the left ventral premotor cortex and the subjectively rated strength of ownership of the stranger's body [13, 15] ($t = 4.33$, $p = 0.038$, corrected; Figure 3C), confirming that activity in this region reflects changes in the subjective feeling of body ownership. Finally, we found increased activity in the bilateral lateral occipital cortices (tentative "extrastriate body area"; see Figure 3A and Table S1), which are known to be involved in the visual processing of body parts [31] and have been consistently observed in previous fMRI studies of limb [15] and whole-body ownership [13] (see the Supplemental Discussion). Together, these findings support the hypothesis that activity in the multisensory premotor-intraparietal cortices is associated with the feeling of ownership of a body seen from the 1PP in a real-world environment.

Decoding Self-Location and Head Direction

To identify brain regions involved in the processing of perceived self-location and head direction, we employed multivoxel pattern analysis [29]. First, we sought evidence for patterns of neural activity that carry information concerning the perceived self-location (position A versus B) in the synchronous and asynchronous conditions. To control for effects that were unrelated to the illusion, such as differences in the 1PP visual input between the positions, we only looked for regions that decoded position A versus B significantly better in the synchronous compared to the asynchronous condition, as well as compared to the chance level (50%; using an inclusive mask thresholded at $p < 0.001$, uncorrected; see the Supplemental Experimental Procedures). We hypothesized that the hippocampus, posterior midline areas, such as the posterior cingulate (PCC) and retrosplenial cortices (RSC), and intraparietal cortex would be involved in representing the perceived self-location. The hippocampus features place cells that encode a rat's allocentric spatial location [20, 32], and human fMRI studies have shown that goal locations in virtual environments can be decoded from this structure [22]. The intraparietal cortex contains egocentric maps of somatosensory and visual space [33–35]

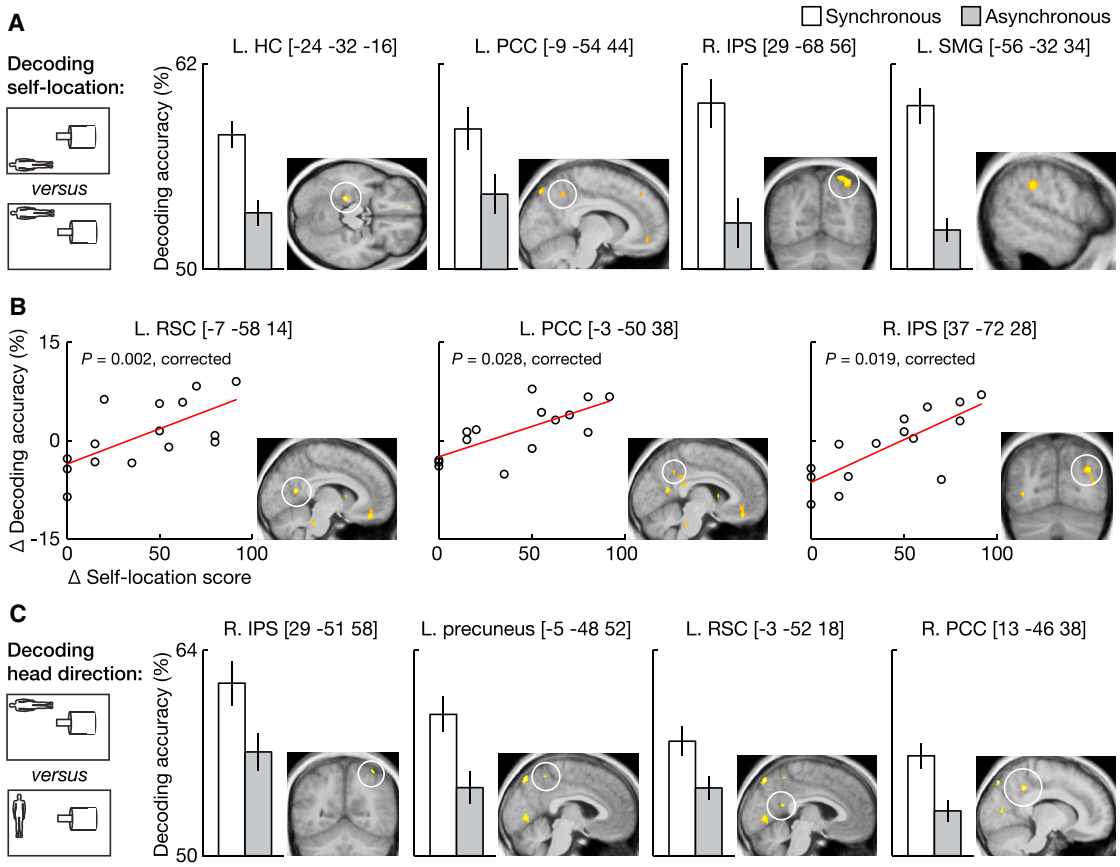

Figure 4. Decoding Self-Location and Head Direction

(A) The perceived self-location could be significantly decoded from patterns of BOLD activity in the hippocampus (HC; see also Figure S4), PCC, cortices lining the IPS, and supramarginal gyrus (SMG).

(B) The decoding accuracy was significantly related to the subjectively reported self-location score in the RSC, PCC, and IPS. Δ, synchronous versus asynchronous difference.

(C) The perceived head direction could be significantly decoded from BOLD activity patterns in the IPS, precuneus, RSC, and PCC.

For display purposes, the statistical threshold for the activation maps was set to $p < 0.005$, uncorrected. A white circle indicates a cluster containing a significant peak ($p < 0.05$, corrected). Error bars indicate SEM.

and is activated during spatial navigation [21] and imagined changes in the 1PP [36], whereas the PCC and RSC have been implicated in the translation of egocentric-to-allocentric representations of space [33, 34, 37]. Thus, this set of areas is ideally suited to construct a multisensory representation of the spatial location of one's bodily self.

In keeping with our hypotheses, the results revealed significant decoding of self-location in the left hippocampus (t = 7.46, p = 0.001, corrected), left posterior cingulate cortex (PCC; t = 3.65, p = 0.041, corrected), and right IPS (t = 4.84, p = 0.034, corrected) (see Figure 4A). The left hippocampal decoding peak was located on the border between the hippocampus and the parahippocampal gyrus (PHG). The corresponding cluster extended from the left posterior hippocampus into the PHG. In a post hoc analysis, we manually segmented the hippocampus to qualitatively isolate the voxels belonging to the self-location cluster that overlapped with the hippocampus proper. This analysis confirmed the presence of voxels in the left posterior hippocampus proper that significantly decoded self-location (Montreal Neurological Institute [MNI]: −22, −30, −12; t = 4.96, p = 0.006, corrected; Figures S4A and S4B). In addition, we found decoding of self-location in the left supramarginal gyrus of the left inferior parietal cortex at a reduced significance threshold (SMG; t = 5.10, $p < 0.001$, uncorrected for multiple comparisons; Figure 4A). Interestingly, the decoding accuracy was positively correlated with the behavioral self-location score in the left PCC (t = 4.00, p = 0.028, corrected), right IPS (t = 4.32, p = 0.019, corrected), and left retrosplenial cortex (RSC; t = 6.21, p = 0.002, corrected) (Figure 4B). This result suggests that activity patterns in these areas are tightly linked to the subjective sense of self-location.

Second, we sought to identify brain regions involved in the processing of the perceived head direction (position B versus C). Single-cell recordings in navigating rats have revealed head direction cells in the retrosplenial [38, 39] and entorhinal cortices [40], and neuroimaging studies have shown that the posterior midline and intraparietal cortices are involved in representing imagined [41] and navigation-related [25, 26] directions in space. Thus, we expected to find significant decoding in this set of areas. In line with our hypotheses, the results showed that the

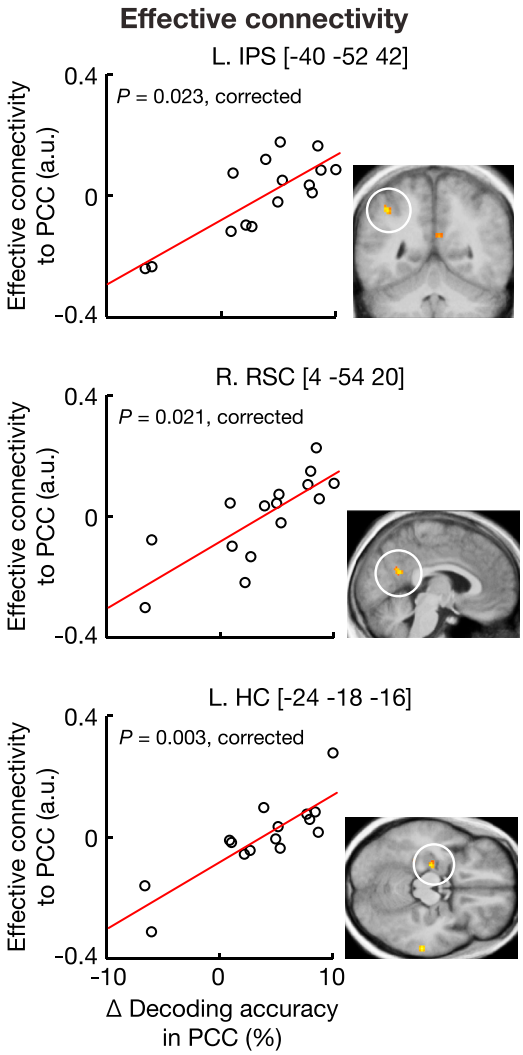

Figure 5. The Neural Interplay between Self-Location and Body Ownership

The graphs show areas that exhibit ownership-related increases in effective connectivity to the PCC that are positively correlated with the PCC decoding accuracy of self-location. The y axis represents changes in connectivity to the PCC induced by the sense of owning the stranger's body viewed from the 1PP (synchronous versus asynchronous across positions), plotted against self-location (position A versus B) decoding accuracy difference (Δ, synchronous versus asynchronous). The results show that the neural representation of self-location in the PCC is significantly associated with ownership-related changes in connectivity strength between the PCC and the IPS, RSC, and hippocampus (HC). For display purposes, the statistical threshold for the activation maps was set to $p < 0.005$, uncorrected. A white circle indicates a cluster containing a significant peak ($p < 0.05$, corrected). See also Figure S4.

perceived head direction could be significantly decoded from the right IPS ($t = 3.56$, $p = 0.047$, corrected), left precuneus ($t = 3.74$, $p = 0.037$, corrected), left RSC ($t = 3.59$, $p = 0.045$, corrected), and right PCC ($t = 4.80$, $p = 0.008$, corrected) (Figure 4C). Thus, fine-grained BOLD activity patterns in the intraparietal, retrosplenial, and posterior cingulate cortices contain information not only on the perceived self-location, but also on the perceived directional heading.

The Neural Interplay between Body Ownership and Self-Location

Finally, we investigated the interplay between the neural representations of body ownership and self-location in terms of the illusion-induced changes in effective connectivity. In the process of localizing one's own body in the environment, the brain must combine information concerning the representation of the body—processed by multisensory areas identified in the premotor-posterior-parietal cortices—with information concerning self-location—encoded in the parieto-hippocampal circuits. We hypothesized that the PCC and RSC play key roles in this integrative process because they have strong anatomical connections to both the intraparietal and medial temporal areas [42] and compute transformations between body-centered and allocentric spatial reference frames [33, 34, 37]. This notion is compatible with our findings showing that activity patterns in the left PCC contained information on self-location (Figure 4A) and that the level of self-location information in the left PCC was positively correlated with the subjectively rated self-location score (Figure 4B). Based on these empirical and theoretical considerations, we chose the left PCC decoding peak as our seed region. We then searched for voxels that displayed ownership-related increases in connectivity to the PCC that were positively related to the PCC decoding accuracy of self-location. Specifically, we performed a psychophysiological interaction (PPI) analysis using the contrast synchronous versus asynchronous across positions as the psychological factor, and searched for voxels in which the PPI parameter estimate significantly co-varied with the PCC decoding accuracy across subjects (see the Supplemental Experimental Procedures for details). This analysis brings together the univariate general linear modeling (GLM) findings related to the feeling of ownership of the body seen from the 1PP (Figure 3) and the multivariate decoding results related to the representation of the perceived self-location. As such, this effective connectivity analysis allowed us to examine the interplay between the neural representations of the body and the perceived self-location. The results showed that participants with higher decoding accuracies of self-location (position A versus B) in the left PCC showed proportionally stronger effective connectivity to the left IPS ($t = 4.38$, $p = 0.023$, corrected), right RSC ($t = 4.46$, $p = 0.021$, corrected), and left hippocampus ($t = 5.93$, $p = 0.003$, corrected) (Figure 5). These findings suggest that ownership of the stranger's body viewed from the 1PP is associated with an effective connectivity increase between the PCC and the intraparietal-retrosplenial-hippocampal cortices that is intimately linked to the representation of self-location in the PCC.

DISCUSSION

In summary, we have used a multisensory full-body illusion involving advanced 3D virtual reality technology in combination with fMRI brain-decoding methods to investigate the relationship between two fundamental components of self-consciousness [5–7]: self-location and body ownership. Our results revealed two novel main findings. First, we found that activity patterns in the IPS, RSC, PCC, and hippocampus reflected the sense of self-location. The illusion of self-location was contingent on the feeling of ownership of the stranger's body from whose

perspective the participants observed the environment. This sense of owning a body viewed from the 1PP was associated with activity in the multisensory premotor-intraparietal cortices. Second, our results suggest that the PCC orchestrates the flow of information concerning bodily self-location between the IPS and the hippocampus. These findings extend beyond previous neuroimaging studies that used full-body illusions [13, 43] but did not investigate the interplay between body ownership and self-location. Similarly, studies based on visual [24] or imagined changes in the 1PP [25, 36] and spatial navigation [22] did not examine whether the spatial representations under investigation contribute to the perceptual experience of self-location or interact with central representations of the body. The present results thus extend our understanding of the role of the posterior parietal and medial temporal cortices in spatial cognition by demonstrating that these areas are not only important for ecological behaviors, such as navigation and perspective-taking, but also support the perceptual representation of the bodily self in space.

Consistent with earlier fMRI studies [13, 15, 44], we found that the sense of owning the stranger's body was associated with activations in the left PMv, bilateral IPS, and LOC (for an in-depth discussion, see the Supplemental Discussion). The intraparietal and premotor cortices are convergence zones for visual, tactile, and proprioceptive information from the body [17], and neuronal populations in these regions continuously integrate multisensory signals to maintain an accurate central representation of one's body in space [7, 44]. We assert that the premotor-intraparietal activations observed in this study reflect the dynamic integration of spatio-temporally congruent visual information from the stranger's body being touched and tactile and proprioceptive signals, resulting in the coherent multisensory percept of the stranger's body being part of the self. This multisensory integrative process could be accompanied by the remapping of peripersonal space from the "disowned" real body to center on the stranger's body viewed from the 1PP, in line with our threat-evoked SCR results (Figures 2 and S3) and a previous study demonstrating such remapping during a single-limb ownership illusion [18]. Finally, we emphasize that our findings go beyond earlier work on body illusions because they reveal a dynamic interaction between fronto-parietal representations of body ownership and parieto-cingulate-hippocampal representations of self-location in the environment (see detailed discussion below).

Our decoding analyses revealed that patterns of BOLD activity in the posterior parietal cortex, PCC, and hippocampus reflect the perceived spatial location of the bodily self. In the posterior parietal cortex, information about self-location could be deciphered from activity patterns in the cortices lining the IPS ($p < 0.05$, corrected) and SMG ($p < 0.001$, uncorrected). The right IPS is particularly interesting because its decoding accuracy was positively related to the reported vividness of the place illusion, suggesting that neural activity in this region reflects the consciously perceived self-location. In the right IPS we also found multivoxel patterns that carried information concerning perceived head direction, and in the IPS bilaterally we observed univariate activations reflecting the feeling of ownership of the stranger's body (see Figure S4E for a post hoc cluster overlap analysis). Previous studies have shown that the IPS contains neuronal populations that encode multimodal signals in various body-centered spatial reference frames [17], including head-centered coordinates [45], as well as retinotopic representations of the visual field [33, 35]. Thus, the IPS is involved in the construction of multisensory representations of the body and its spatial context. These properties and the current results point to the IPS as a good candidate to support an egocentric representation of self-location. We propose that the place- and head-direction-specific patterns detected in the right IPS reflect the dynamic updating of an egocentric spatial reference frame that is anchored to the perceived location and orientation of one's own body in space.

The decoding accuracy in the PCC and RSC also mirrored the subjectively reported self-location score, indicating that these regions may play key roles in supporting the sense of self-location. Although relatively little is known about the cognitive functions of the PCC, this region is a central node in the "default mode network" and activity in this structure has been associated with decision-making, attention, memory, face perception, and spatial navigation [46–48]. The RSC (Brodmann areas 29 and 30), which together with the PCC (areas 23 and 31) constitutes the "retrosplenial complex" [37], has also been implicated in memory processing and navigation [38]. Interestingly, RSC lesions in humans impair the ability to represent one's directional heading with respect to environmental landmarks [49]. This is compatible with our observation that the PCC and RSC elaborate information on the perceived head direction. As previously mentioned, the PCC and the RSC are anatomically interconnected with the intraparietal cortex and medial temporal regions [42] and are thought to mediate the translation between egocentric and allocentric spatial representations [34, 38]. Our effective connectivity analysis revealed illusion-specific changes in the functional coupling between the PCC and nodes in the IPS, RSC, and hippocampus that were positively correlated with the information content concerning self-location in the PCC (also see Figures S4C and S4D for effective connectivity results with respect to head direction). This observation suggests that the interplay between these brain areas reflects the coordinated processing of information encompassing both the body and the perceived self-location. Thus, these findings are compatible with the notion that the PCC and the RSC work in concert with the IPS and the hippocampus to represent the perceived spatial location of the bodily self. We propose that the role of the PCC and the RSC in this process may consist of translating egocentric intraparietal into allocentric hippocampal multisensory representations of self-location.

Studies on spatial memory have shown that the human brain uses both egocentric and allocentric representations of space and that regions in the medial temporal lobe contribute primarily to the latter [34]. We found that BOLD activity patterns in the hippocampus contained information concerning the perceived spatial location of one's bodily self. However, we found no evidence of head direction decoding in this structure. In light of this, we propose that the hippocampus supports an allocentric representation of the perceived self-location and that—in line with our effective connectivity results—this representation is intimately linked to the egocentric representation of self-location in the IPS via intermediate processing in the PCC. Population activity of hippocampal place cells form the likely neuronal

underpinning for the multivoxel patterns that we observed in this region. These cells have been shown to represent the animal's position in allocentric spatial reference frames, at the level of both neuronal spikes [20] and spatially distributed local field potentials [50]. The proposed role of the hippocampus in constructing an allocentric representation of self-location fits well with earlier studies on spatial navigation and path integration, in which the locations of the participants' targets in virtual navigation tasks can be decoded from hippocampal activity patterns [22]. Our results extend the understanding of the role of the hippocampus in spatial cognition by demonstrating that hippocampal activity patterns reflect the currently perceived self-location and that multisensory integrative mechanisms related to body ownership can update this representation even in the absence of active navigation and path integration.

Our experimentally induced out-of-body illusion shares some key characteristics with OBEs elicited by focal epilepsy and electrical brain stimulation [9–11]. In both cases, the spatial location of the self is perceived at an extracorporeal position with respect to the real body viewed from a visual 3PP. In contrast to the illusion, clinical OBEs are often related to changes in the perceived location of the self with respect to the gravitational field and various vestibular sensations such as floating and rotation [11]. A previous neuroimaging study investigated the interaction between self-location and the perceived direction of the 1PP in healthy participants and presented evidence for the involvement of the bilateral posterior superior temporal gyrus (pSTG) [43]. In addition, direct electrical stimulation of the right angular gyrus in one patient elicited a complex body illusion featuring vestibular sensations and changes in body posture [11]. We speculate that the absence of significant decoding of self-location in the pSTG and angular gyrus in our study could be explained by the fact that our paradigm did not involve manipulations of self-orientation with respect to the gravitational field. We further speculate that the representations of self-location and body ownership characterized in the present study might interact with vestibular representations of self-orientation in the pSTG and angular gyrus to represent the full range of possible positions of one's body in 3D space with six degrees of freedom.

In conclusion, this study has shed light on the mechanisms by which the senses of self-location and body ownership are combined in the human brain to build the coherent experience of being a body *somewhere* in space. Our results suggest that an interconnected set of regions in the hippocampus and the posterior cingulate, retrosplenial, and intraparietal cortices plays an important role in the construction of this fundamental subjective feeling of self. The characterization of these neural processes lies at the heart of neuroscience and psychology because the experience of one's own body and its location in the environment defines the origin of the egocentric reference frame that is necessary for human self-consciousness [5, 51] and our behavioral interactions with the external environment [2].

EXPERIMENTAL PROCEDURES

Participants

Fifteen naive healthy human volunteers (ages 21–33, mean age ± SD = 27 ± 3 years; six females) participated in the study. Informed consent was obtained prior to the experimental sessions. The Regional Ethical Review Board of Stockholm approved the study.

Illusion Induction

For induction of the illusory feeling of ownership of the stranger's body seen from the 1PP, a white spherical object (6.5 cm in diameter) attached to a 1-m-long wooden stick (Figure 1) repetitively touched the abdomen, right upper leg, and left foot of the stranger's body in the HMDs while the participant received temporally congruent tactile stimulation on the corresponding body parts. In the asynchronous control condition, the tactile stimulation was delayed by 1 s with respect to the touches of the stranger's body in the HMDs. The stereoscopic visual stimuli were presented in a set of MR-compatible HMDs (Nordic Neurolab). See the Supplemental Experimental Procedures for details on the experimental setup and the visuotactile stimulation protocols and Movie S1 for a sample clip from position A.

Illusion Quantification

To quantify the illusion experience, we used three separate psychometric or psychophysiological measurements. Concurrently with the brain scanning, we examined SCR evoked by threats directed toward the stranger's body or the real body using a MR-compatible SCR-recording module (Brain Products) [30]. Immediately after the brain scanning, the participants were presented with additional repetitions of each experimental condition and asked to complete a self-location task and a questionnaire (in two separate sessions) to quantify the subjective feeling of self-location and body ownership, respectively. For details, see the Supplemental Experimental Procedures.

fMRI

Functional imaging data (voxel size 2 × 2 × 2 mm^3) were collected using a Siemens TIM Trio 3T scanner. For the decoding analyses, the image volumes were analyzed in native space after standard preprocessing. Within each participant, we used locally multivariate mapping with support vector machine classifiers to identify multivoxel patterns [29]. The resulting decoding maps were spatially normalized to the standard MNI space and entered into a second-level analysis, using the Statistical Parametric Mapping software (SPM8) (for details, see the Supplemental Experimental Procedures). For the univariate GLM analysis, the image volumes were preprocessed, spatially normalized, and analyzed with standard procedures using SPM8 (see the Supplemental Experimental Procedures). In all of the fMRI analyses (multivariate and univariate), we employed a voxel-wise whole-brain approach. First, the whole-brain activation maps were thresholded at $p < 0.005$ (uncorrected for multiple comparisons) and overlaid onto orthogonal sections of the average structural scan generated from the 15 subjects (Figures 3, 4, and 5). For the statistical inference, we applied corrections for multiple comparisons within the appropriate search space for the contrast of interest using the family-wise error rate correction implemented in SPM8. In areas for which we had a priori hypotheses, we applied correction for multiple comparisons within spheres defined around peaks from previous relevant studies on body ownership and spatial cognition ("small-volume correction"; see the Supplemental Experimental Procedures). For areas outside the hypothesized regions, we corrected for multiple comparisons using the whole brain as search space (however, no such activations were observed). In a purely descriptive manner, we also report the uncorrected p value for strong activations ($p < 0.001$, uncorrected) that did not survive correction at the whole-brain level (Tables S1–S3). For all activations, the coordinates of the peak voxel are given in the MNI standard space (x, y, z).

Eye Tracking

The participants' eye movements were tracked throughout the experiment to rule out potential systematic differences in gaze between the conditions that might confound the results. For details and results, see the Supplemental Experimental Procedures and Figure S5.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Discussion, Supplemental Experimental Procedures, five figures, three tables, and one movie and

can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.03.059.

AUTHOR CONTRIBUTIONS

A.G. and H.H.E. developed the study concept. All authors contributed to the study design. Testing and data collection were performed by A.G. and G.G. M.B. performed the multivoxel pattern analysis. A.G. and G.G. performed the rest of the data analyses. A.G. drafted the manuscript and wrote it together with H.H.E.; M.B. and G.G. provided important revisions. All authors approved the final version of the manuscript for submission.

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REFERENCES

1. James, W. (1890). The Principles of Psychology. (New York: Henry Holt).
2. Graziano, M., and Botvinick, M. (2002). How the brain represents the body: insights from neurophysiology and psychology. Common Mech. Percept. Action Atten. Perform. *19*, 136–157.
3. Merleau-Ponty, M. (1945). Phénoménologie de la Perception. (Paris: Gallimard).
4. Rochat, P. (1995). The Self in Infancy: Theory and Research. (Elsevier).
5. Blanke, O., and Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. Trends Cogn. Sci. *13*, 7–13.
6. Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A., and Lopez, C. (2013). Bodily ownership and self-location: components of bodily self-consciousness. Conscious. Cogn. *22*, 1239–1252.
7. Ehrsson, H.H. (2012). The concept of body ownership and its relation to multisensory integration. In The Handbook of Multisensory Processes, B. Stein, ed. (Cambridge: MIT Press).
8. Vallar, G., and Ronchi, R. (2009). Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. Exp. Brain Res. *192*, 533–551.
9. Penfield, W., and Erickson, T.C. (1941). Epilepsy and Cerebral Localization. (Oxford: Charles C. Thomas).
10. De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T., and Van de Heyning, P. (2007). Visualizing out-of-body experience in the brain. N. Engl. J. Med. *357*, 1829–1833.
11. Blanke, O., Landis, T., Spinelli, L., and Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. Brain *127*, 243–258.
12. Ehrsson, H.H. (2007). The experimental induction of out-of-body experiences. Science *317*, 1048.
13. Petkova, V.I., Björnsdotter, M., Gentile, G., Jonsson, T., Li, T.-Q., and Ehrsson, H.H. (2011). From part- to whole-body ownership in the multisensory brain. Curr. Biol. *21*, 1118–1122.
14. Botvinick, M., and Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. Nature *391*, 756.
15. Ehrsson, H.H., Spence, C., and Passingham, R.E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. Science *305*, 875–877.
16. Graziano, M.S.A., Hu, X.T., and Gross, C.G. (1997). Visuospatial properties of ventral premotor cortex. J. Neurophysiol. *77*, 2268–2292.
17. Graziano, M.S.A., Cooke, D.F., and Taylor, C.S. (2000). Coding the location of the arm by sight. Science *290*, 1782–1786.
18. Brozzoli, C., Gentile, G., and Ehrsson, H.H. (2012). That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. J. Neurosci. *32*, 14573–14582.
19. Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-ownership. Neuropsychologia *48*, 703–712.
20. O'Keefe, J., and Nadel, L. (1978). The Hippocampus as a Cognitive Map. (Oxford: Oxford University Press).
21. Maguire, E.A., Burgess, N., Donnett, J.G., Frackowiak, R.S., Frith, C.D., and O'Keefe, J. (1998). Knowing where and getting there: a human navigation network. Science *280*, 921–924.
22. Hassabis, D., Chu, C., Rees, G., Weiskopf, N., Molyneux, P.D., and Maguire, E.A. (2009). Decoding neuronal ensembles in the human hippocampus. Curr. Biol. *19*, 546–554.
23. Moser, E.I., Kropff, E., and Moser, M.-B. (2008). Place cells, grid cells, and the brain's spatial representation system. Annu. Rev. Neurosci. *31*, 69–89.
24. Vass, L.K., and Epstein, R.A. (2013). Abstract representations of location and facing direction in the human brain. J. Neurosci. *33*, 6133–6142.
25. Marchette, S.A., Vass, L.K., Ryan, J., and Epstein, R.A. (2014). Anchoring the neural compass: coding of local spatial reference frames in human medial parietal lobe. Nat. Neurosci. *17*, 1598–1606.
26. Doeller, C.F., Barry, C., and Burgess, N. (2010). Evidence for grid cells in a human memory network. Nature *463*, 657–661.
27. Chadwick, M.J., Jolly, A.E.J., Amos, D.P., Hassabis, D., and Spiers, H.J. (2015). A goal direction signal in the human entorhinal/subicular region. Curr. Biol. *25*, 87–92.
28. Guterstam, A., and Ehrsson, H.H. (2012). Disowning one's seen real body during an out-of-body illusion. Conscious. Cogn. *21*, 1037–1042.
29. Kriegeskorte, N., Goebel, R., and Bandettini, P. (2006). Information-based functional brain mapping. Proc. Natl. Acad. Sci. USA *103*, 3863–3868.
30. Ehrsson, H.H., Wiech, K., Weiskopf, N., Dolan, R.J., and Passingham, R.E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. Proc. Natl. Acad. Sci. USA *104*, 9828–9833.
31. Downing, P.E., Jiang, Y., Shuman, M., and Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. Science *293*, 2470–2473.
32. Aronov, D., and Tank, D.W. (2014). Engagement of neural circuits underlying 2D spatial navigation in a rodent virtual reality system. Neuron *84*, 442–456.
33. Kravitz, D.J., Saleem, K.S., Baker, C.I., and Mishkin, M. (2011). A new neural framework for visuospatial processing. Nat. Rev. Neurosci. *12*, 217–230.
34. Burgess, N. (2008). Spatial cognition and the brain. Ann. N Y Acad. Sci. *1124*, 77–97.
35. Sereno, M.I., Pitzalis, S., and Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. Science *294*, 1350–1354.
36. Lambrey, S., Doeller, C., Berthoz, A., and Burgess, N. (2012). Imagining being somewhere else: neural basis of changing perspective in space. Cereb. Cortex *22*, 166–174.
37. Epstein, R.A. (2008). Parahippocampal and retrosplenial contributions to human spatial navigation. Trends Cogn. Sci. *12*, 388–396.
38. Vann, S.D., Aggleton, J.P., and Maguire, E.A. (2009). What does the retrosplenial cortex do? Nat. Rev. Neurosci. *10*, 792–802.
39. Chen, L.L., Lin, L.H., Green, E.J., Barnes, C.A., and McNaughton, B.L. (1994). Head-direction cells in the rat posterior cortex. I. Anatomical distribution and behavioral modulation. Exp. Brain Res. *101*, 8–23.
40. Sargolini, F., Fyhn, M., Hafting, T., McNaughton, B.L., Witter, M.P., Moser, M.-B., and Moser, E.I. (2006). Conjunctive representation of position, direction, and velocity in entorhinal cortex. Science *312*, 758–762.
41. Schindler, A., and Bartels, A. (2013). Parietal cortex codes for egocentric space beyond the field of view. Curr. Biol. *23*, 177–182.

42. Kobayashi, Y., and Amaral, D.G. (2007). Macaque monkey retrosplenial cortex: III. Cortical efferents. J. Comp. Neurol. *502*, 810–833.

43. Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R., and Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. Neuron *70*, 363–374.

44. Gentile, G., Guterstam, A., Brozzoli, C., and Ehrsson, H.H. (2013). Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. J. Neurosci. *33*, 13350–13366.

45. Avillac, M., Denève, S., Olivier, E., Pouget, A., and Duhamel, J.R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. Nat. Neurosci. *8*, 941–949.

46. Leech, R., and Sharp, D.J. (2014). The role of the posterior cingulate cortex in cognition and disease. Brain *137*, 12–32.

47. Pearson, J.M., Heilbronner, S.R., Barack, D.L., Hayden, B.Y., and Platt, M.L. (2011). Posterior cingulate cortex: adapting behavior to a changing world. Trends Cogn. Sci. *15*, 143–151.

48. Apps, M.A.J., Tajadura-Jiménez, A., Sereno, M., Blanke, O., and Tsakiris, M. (2015). Plasticity in unimodal and multimodal brain areas reflects multisensory changes in self-face identification. Cereb. Cortex *25*, 46–55.

49. Aguirre, G.K., and D'Esposito, M. (1999). Topographical disorientation: a synthesis and taxonomy. Brain *122*, 1613–1628.

50. Agarwal, G., Stevenson, I.H., Berényi, A., Mizuseki, K., Buzsáki, G., and Sommer, F.T. (2014). Spatially distributed local fields in the hippocampus encode rat position. Science *344*, 626–630.

51. Vogeley, K., and Fink, G.R. (2003). Neural correlates of the first-person-perspective. Trends Cogn. Sci. *7*, 38–42.